



REPLY TO DEES ET AL.:

Ocean warming promotes species-specific increases in the cellular growth rates of harmful algal blooms

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Recently, we (1) reported that, since 1982, several regions across the North Atlantic and North Pacific Oceans have experienced warming in specific seasons and locations that have significantly increased the potential cellular growth rates and bloom seasons of two harmful algae, *Alexandrium fundyense* and *Dinophysis acuminata*, and that new blooms caused by these species have emerged in these same regions. In their comment “Harmful algal blooms in the Eastern North Atlantic Ocean,” Dees et al. (2) examine the Continuous Plankton Recorder data from the North Eastern Atlantic and North Sea from 1982 to 2015 and find no relationship between *Dinophysis* spp. abundance and sea-surface temperature. This observation is consistent with the conclusions of our original publication (1) and with two central tenants of algal ecology.

First, phytoplankton display a great range of physiological and trait-specific plasticity across species and strains (3). Indeed, during our study (1) we limited the application of our *Alexandrium* models to the strains within *Alexandrium* group I (now *Alexandrium catenella*) only, as other species of *Alexandrium* display broad differences in a multitude of characteristics, including the temperature-dependence of growth rates (4). With regard to *Dinophysis*, we focused solely on the species *D. acuminata*, as there are significant differences among *Dinophysis* spp. with regard to many aspects of their physiology, such as their general reliance on phagotrophy compared to phototrophy (5, 6) and temperature tolerances (5). Because the Continuous Plankton Recorder does not provide species-level information, Dees et al. (2) only

examined *Dinophysis* at the genus level. Such a lumping of species into a single genus masks trends among the many individual *Dinophysis* spp. present in the region (7), each of which is likely to differ in their temperature-dependent growth rates (5). Such an approach (2) would be unlikely to reveal the species-specific trends our model depicted.

A second central tenant of algal ecology that is well-supported by the observations of Dees et al. (2), and was featured prominently in our original publication (1), is that blooms occur as a function of growth exceeding loss rates within a given ecosystem. While temperatures that maximize harmful algal bloom (HAB) growth create the potential for blooms, actual bloom occurrence depends upon additional factors (8). Dees et al. (2) examined abundances of *Dinophysis* spp. and assumed the enhanced growth our models depicted would be manifested as higher cell abundances, an outcome requiring concurrent biological and physical loss rates to remain unchanged. Given the strong effect temperature has on key processes, such as zooplankton grazing (9) and stratification (10), it would be expected that there are regions of the ocean where temperature-facilitated increases in cellular growth rates of harmful algae have been offset by concurrent increases in loss rates. Although the occurrence of HABs is controlled by multiple processes, temperature is a central organizing factor (11). Our models (1) and dozens of observations cited in our study indicate increasing ocean temperatures have facilitated an expansion of *A. fundyense* and *D. acuminata* blooms in regions across the North Atlantic and North Pacific Oceans.

1 Gobler CJ, et al. (2017) Ocean warming since 1982 has expanded the niche of toxic algal blooms in the North Atlantic and North Pacific oceans. *Proc Natl Acad Sci USA* 114:4975–4980.

2 Dees P, et al. (2017) Harmful algal blooms in the Eastern North Atlantic Ocean. *Proc Natl Acad Sci USA* 114:E9763–E9764.

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